

Description of a New Species of the Asian Newt Genus *Tylototriton sensu lato* (Amphibia: Urodela: Salamandridae) from Southwest China

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Abstract The newt genus *Tylototriton sensu lato* is widely distributed in Eastern, Southeastern and Southern Asia. Previous studies indicated that there still has been several cryptic species in the group. Here, we describe a new species of the genus from Guizhou Province, China. Phylogenetic analyses based on mitochondrial DNA supported that the new species was resolved as an independent clade nested into the *Tylototriton sensu lato* clade. On morphology, the new species could be distinguished from its congeners by a combination of the following characters: large body size (SVL 76.8–85.2 mm in male and 76.3–87.4 mm in female); head longer than wide; snout truncate in dorsal view; tail length longer than the snout-vent length in males; the distal digit ends, ventral digits, peripheral area of cloaca and the tail's lower margin are orange; relative length of toes III > IV > II > I > V; the distal tips of the limbs greatly overlapping when the fore and hind limbs are pressed along the trunk; fingertips reach the level beyond the snout when the forelimbs are stretched forward.

Keywords China, molecular phylogenetic analysis, new species, newts, taxonomy

1. Introduction

The Asian newt genus *Tylototriton sensu lato* Anderson, 1871 is widely distributed from the eastern Himalayas, Indochina, to central and southern China (Fei and Ye, 2016; Frost, 2020). The taxonomic assignments of the group have been much controversial. Fei *et al.* (2005) divided the genus into two species groups, i.e. the *T. verrucosus* Anderson, 1871 species group and the *T. asperrimus* Unterstein, 1930 species group. Dubois and Raffaelli (2009) upgraded the two groups as two subgenera *Tylototriton* and *Yaotriton*. Fei *et al.* (2012) further classified all members of *T. sensu lato* into three genera, *T. sensu stricto*, *Yaotriton* and *Liangshantriton* (a new genus containing one species *L. taliangensis* Liu, 1950). Fei *et al.* (2016) further classified the members of *T. sensu stricto* defined by Fei and Ye (2016) into two subgenera, *Tylototriton* and *Qianotriton* (a new subgenus). Whatever, *T. sensu lato* was strongly resolved to be a monophyletic group by most molecular phylogenetic studies (e.g., Nishikawa *et al.*, 2013a, 2013b; Wang *et al.*, 2018).

In currently known 25 species of *T. sensu lato*, 17 species have been described in the last decade, and even ten species have been described in the past five years (Frost, 2020). This led to the underrepresented systematic arrangements in previous studies especially in the species group with wide distributional ranges. For example, systematic profiles of the *T. asperrimus* species group have been continually changed, and the distributional range of *T. asperrimus* has been gradually defined to be more narrowed, because many populations ever identified as *T. asperrimus* were found to be separated

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species (e.g., *T. anhuiensis* Qian, Sun, Li, Guo, Pan, Kang, Wang, Jiang, Wu, and Zhang, 2017, *T. broadoridgus* Shen, Jiang, and Mo, 2012, *T. dabienicus* Chen, Wang, and Tao, 2010, *T. liuyangensis* Yang, Jiang, Shen, and Fei, 2014, and *T. wenxianensis* Fei, Ye, and Yang, 1984). More remarkably, many new species were clustered into one apart clade (corresponding to the “*T. wenxianensis*” clade as Clade V in Wang *et al.* 2018), distinctly from the true “*T. asperrimus*” clade (corresponding to Clade IV in Wang *et al.*, 2018). In Wang *et al.* (2018), the “*T. wenxianensis*” clade contained *T. wenxianensis*, *T. dabienicus*, *T. broadoridgus*, *T. liuyangensis*, *T. lizhenchangii* and three putative cryptic species. The three putative cryptic species occur from Dabie Mountains of Anhui Province, Wufeng County of Hubei Province and Libo County of Guizhou Province, respectively. The population from Dabie Mountains was already described as a new species *T. anhuiensis* (Qian *et al.*, 2017). But the other two have not been investigated in detail and furtherly described.

In 2018, we collected some specimens of *T. sensu lato* from Maolan National Nature Reserve in Libo County, Guizhou Province, China. Phylogenetic analyses and morphological comparisons indicated that the population was distinctly different from its congeners. Herein we describe it as a new species.

2. Materials and Methods

2.1. Specimen A total of nine specimens of the undescribed species including two females, six males and one larvae (for voucher information see Tables 1 and S1) were collected from Maolan National Nature Reserve in Libo County, Guizhou Province, China (Figure 1). In the field, after taking photographs, the newts were euthanized using isoflurane, and then the specimens were fixed in 10% buffered formalin. Tissue samples were taken and preserved separately in 95% ethanol prior to fixation. The specimens were deposited in Chengdu Institute of Biology (CIB), Chinese Academy of Sciences (CAS). The Animal Care and Use Committee of CIB, CAS provided full approval for this research (Number: CIB2013041103). Field experiments were approved by the Management Office of Maolan National Nature Reserve, Guizhou Province, China (Project number: 201102034).

2.2. Molecular data and phylogenetic analyses

Total DNA was extracted from tissue samples of five specimens of the undescribed species using a standard proteinase phenol-chloroform protocol (Sambrook *et al.*, 1989). The mitochondrial 16S rRNA and NADH dehydrogenase subunit 2 (ND2) genes were amplified,

the primers P7 (5'-CGCCTGTTTACCAAAAACAT-3'), P8 (5'-CCGGTCTGAACTCAGATCACGT-3') and SL-1 (5'-ATAGAGGTTCAAACCCTCTC-3'), SL-2 (5'-TTAAAGTGTCTGGGTTGCATTTCAG-3') were used for 16S rRNA and ND2 following Simon *et al.* (1994) and Shen *et al.* (2012), respectively. They were amplified under the following conditions: an initial denaturing step at 95 °C for 4 min; 36 cycles of denaturing at 95 °C for 30 s, annealing at 52 °C (for 16S)/58 °C (for ND2) for 40 s and extending at 72 °C for 70 s, and a final extending step of 72 °C for 10 min. Sequencing was conducted using an ABI3730 automated DNA sequencer in Shanghai DNA BioTechnologies Co., Ltd. (Shanghai, China). All new sequences were deposited in GenBank (for accession numbers see Table 1).

For phylogenetic analyses, the available sequence data for all species of the genus *Tylotriton* were downloaded from GenBank (for accession numbers see Table 1). Corresponding sequences of one *Pachytriton labiatus*, one *Pleurodeles waltl* and one *Echinotriton chinhaiensis* were downloaded (for GenBank accession numbers see Table 1), and *Pachytriton labiatus* was used as outgroup according to the previous study (Qian *et al.*, 2017; Wang *et al.*, 2018).

Sequences were assembled and aligned using the ClustalW module in BioEdit v. 7.0.9.0 (Hall, 1999) with default settings. Alignments were checked by eye and revised manually if necessary. To avoid bias in alignments, the regions of defined sequence conservation were extracted from the length-variable 16S gene fragments using GBLOCKS v. 0.91.b (Castresana, 2000) with default settings. Non-sequenced fragments were defined as missing loci.

Phylogenetic relationships were reconstructed based on the mitochondrial gene concatenated dataset. Phylogenetic analyses were conducted using maximum likelihood (ML) and Bayesian Inference (BI) methods, implemented in PhyML v. 3.0 (Guindon *et al.*, 2010) and MrBayes v. 3.12 (Ronquist and Huelsenbeck, 2003), respectively. To avoid under- or over-parameterization (Lemmon and Moriarty, 2004; McGuire *et al.*, 2007), the best partition scheme and the best evolutionary model for each partition were chosen for the phylogenetic analyses using PARTITIONFINDER v. 1.1.1 (Robert *et al.*, 2012). In this analysis, 16S gene and each coding position of ND2 gene were defined and Bayesian Inference Criteria was used. As a result, the analysis suggested that the best partition scheme is 16S gene + (first + second) coding positions of ND2 gene + the third coding positions of ND2 gene, and selected TrN + I + G model as the best model for each partition. For the ML tree, branch

Table 1 Information of samples used in the molecular analyses in this study.

Sample ID	Species	Voucher No.	Locality	GenBank accession No.	
				16S rRNA	ND2
1	<i>Tylototriton maolanensis</i> sp. nov.	CIBWg20090730002	Libo Co., Guizhou Prov., China	KY800576	KY800843
2	<i>Tylototriton maolanensis</i> sp. nov.	CIBWg20090730003	Libo Co., Guizhou Prov., China	KY800577	KY800844
3	<i>Tylototriton maolanensis</i> sp. nov.	CIBML20180427003	Libo Co., Guizhou Prov., China	MK835789	MK820701
4	<i>Tylototriton maolanensis</i> sp. nov.	CIBML20180427004	Libo Co., Guizhou Prov., China	MK835790	MK820702
5	<i>Tylototriton maolanensis</i> sp. nov.	CIBML20180427001	Libo Co., Guizhou Prov., China	MK835787	MK820699
6	<i>Tylototriton maolanensis</i> sp. nov.	CIBML20180427002	Libo Co., Guizhou Prov., China	MK835788	MK820700
7	<i>Tylototriton maolanensis</i> sp. nov.	CIBML2019015001	Libo Co., Guizhou Prov., China	MK835791	MK820703
8	<i>Tylototriton maolanensis</i> sp. nov.	CIBWg20090730001	Libo Co., Guizhou Prov., China	KY800575	KY800842
9	<i>Tylototriton maolanensis</i> sp. nov.	CIBWg20090730005	Libo Co., Guizhou Prov., China	KY800578	KY800845
10	<i>Tylototriton maolanensis</i> sp. nov.	CIBWg20090730004	Libo Co., Guizhou Prov., China	KY800580	KY800846
11	<i>Tylototriton broadoridgus</i>	CIB200084	Sangzhi Co., Hunan Prov., China	KY800570	KY800837
12	<i>Tylototriton dabienicus</i>	HNNU1004-024	Shangcheng Co., Anhui Prov., China	KY800608	KC147812
13	<i>Tylototriton dabienicus</i>	HNNU 1004-015	Shangcheng Co., Anhui Prov., China	KY800607	KC147811
14	<i>Tylototriton dabienicus</i>	HNNU 1004-026	Shangcheng Co., Anhui Prov., China	KY800609	KY800869
15	<i>Tylototriton anhuiensis</i>	CIB08042905-2	Yuexi Co. Anhui Prov., China	KY800587	KY800853
16	<i>Tylototriton anhuiensis</i>	CIB 08042905-3	Yuexi Co. Anhui Prov., China	KY800588	KY800854
17	<i>Tylototriton anhuiensis</i>	CIB 08042905-4	Yuexi Co. Anhui Prov., China	KY800589	KY800855
18	<i>Tylototriton wenxianensis</i>	CIB20090527	Wenxian Co., Gansu Prov., China	KY800579	KC147813
19	<i>Tylototriton wenxianensis</i>	CIB 2010123101	Pingwu Co., Gansu, China	KY800604	KY800867
20	<i>Tylototriton wenxianensis</i>	CIB 2010123102	Pingwu Co., Gansu, China	KY800605	KY800868
21	<i>Tylototriton wenxianensis</i>	CIB 20070639	Qingchuan Co., Sichuan, China	KY800542	KY800815
22	<i>Tylototriton liuyangensis</i>	CIB110601F06	Liuyang City, Hunan Prov., China	KY800615	KY800875
23	<i>Tylototriton lizhenchangii</i>	KUHE:42316	Yizhang Co., Hunan Prov., China	KY800621	KY800881
24	<i>Tylototriton panhai</i>	NUOL 00421	/	/	KT304310
25	<i>Tylototriton vietnamensis</i>	IEBRA.0701	Mauson, Lang Son Prov., Vietnam	KY800613	KY800873
26	<i>Tylototriton hainanensis</i>	CIB20081048	Mt. Diaoluo, Hainan Prov., China	KY800553	KC147817
27	<i>Tylototriton notialis</i>	VNMNTAO1229	Pu Hoat, Nghe An, Vietnam	/	KY800883
28	<i>Tylototriton asperrimus</i>	CIBGX20080714	Jinxiu Co., Guangxi, China	KY800546	KY800819
29	<i>Tylototriton zieglerei</i>	VNMN3390	Quan Ba, Ha Giang, Vietnam	KY800625	KY800889
30	<i>Tylototriton verrucosus</i>	CIB-TSHS1	Longchuan Co., Dehong state, Yunnan Prov., China	KY800581	KY800847
31	<i>Tylototriton shanjing</i>	CIB980004	Baoshan City, Yunnan Prov., China	KY800562	KY800831
32	<i>Tylototriton pulcherrimus</i>	KUHE:46406	Pet Trade	KY800620	KY800880
33	<i>Tylototriton podichthys</i>	NCSM 77725	/	/	KT304295
34	<i>Tylototriton uyenoi</i>	KUHE:19147	Doi Suthep, Chiang Mai, Thailand	/	AB830733
35	<i>Tylototriton anguliceps</i>	NUOL 00420	/	/	KT304301
36	<i>Tylototriton yangi</i>	KUHE:42282	Pet Trade	KY800624	KY800887
37	<i>Tylototriton shanorum</i>	KUHE 42348	Shan State, Myanmar	/	AB769544
38	<i>Tylototriton ngarsuensis</i>	LSUHC13762	Shan State, Myanmar	/	MH836585
39	<i>Tylototriton himalayanus</i>	CIB201406246	Mai Pokhari, Illam, Mechi, Nepal	KY800590	KT765173
40	<i>Tylototriton kachinorum</i>	ZMMU A5953	Ingyin Taung Mt., Indawgyi, Kachin, Myanmar	MK095618	/
41	<i>Tylototriton kweichowensis</i>	CIBWg20080818014	Bijie City, Guizhou Prov., China	KY800551	KY800823
42	<i>Tylototriton taliangensis</i>	CIBGG200110183	Shimian Co., Ya'an City, Sichuan Prov., China	KY800559	KC147819
43	<i>Tylototriton pseudoverrucosus</i>	CIBWCG2012003	Ningnan Co., Liangshanyizu State, Sichuan Prov., China	KY800597	KY800861
44	<i>Echinotriton chinhaiensis</i>	CIBZHJY2	Zhenhai Co., Zhejiang Prov., China	KY800628	KY800892
45	<i>Pachytriton labiatus</i>	/	/	EU880325	EU880325
46	<i>Pleurodeles waltl</i>	/	Cadiz, Andalusia, Spain	EU880330	EU880330

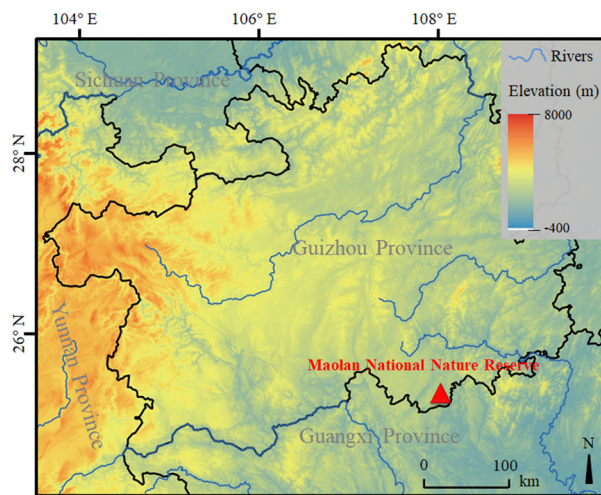


Figure 1 The type locality of *Tylototriton maolanensis* sp. nov., Maolan National Nature Reserve, Libo County, Guizhou Province, China.

supports were drawn from 10,000 nonparametric bootstrap replicates. In BI analyses, the parameters for each partition were unlinked, and branch lengths were allowed to vary proportionately across partitions. Two runs each with four Markov chains were simultaneously run for 50 million generations with sampling every 1,000 generations. The first 25% trees were removed as the “burn-in” followed by calculations of Bayesian posterior probabilities and the 50% majority-rule consensus of the post burn-in trees sampled at stationarity. Genetic distance between *Tylototriton* species was calculated with uncorrected *p*-distance model on ND2 gene using MEGA v. 6.06 (Tamura *et al.*, 2013).

2.3. Morphological comparison Eight specimens of the undescribed species, seven *T. wenxianensis* from two localities, three *T. broadoridgus* from its type locality (Sangzhi County, Hunan Province, China) and four *T. dabienicus* from its type locality (Shangcheng County, Henan Province, China) were examined and measured (Table S1). The terminology and methods followed Fei (1999). Measurements of *T. anhuiensis* were retrieved from Qian *et al.* (2017).

Measurements were taken with a dial caliper to 0.1 mm. Twenty morphometric characters of adult specimens were measured: total length (TOL, distance from tip of snout to tip of tail); snout-vent length (SVL, distance from tip of snout to posterior edge of vent); head length (HDL, distance from jugular fold to snout tip); head width (HDW, maximum head width); snout length (SL, distance from tip of snout to the anterior corner of eye); eye diameter (ED, distance from the anterior corner to the posterior corner of the eye); interorbital distance (IOD, minimum distance between the eyes); upper eyelid width (UEW,

greatest width of the upper eyelid margins measured perpendicular to the anterior-posterior axis); internasal distance (IND, minimum distance between the external nares); IFE (distance between anterior corner of eyes); IAE (distance between posterior corner of eyes); trunk length (TRL, from gular fold of throat to anterior tip of vent); tail length (TAL, from anterior tip of cloaca to tip of tail); tail height (TH, maximum tail height); length of lower arm (LLA, distance from elbow to tip of wrist); hand length (HL, wrist from elbow to longest finger); the third finger length (FIIL, distance from base to tip of finger III); thigh length (TLH, distance from groin to knee); tibia length (TL, distance from knee to tarsus); and the third toe length (TIIL, distance from base to tip of toe III).

Only one larvae of the undescribed species (voucher number: CIBML2019015001) was collected and measured. Ten morphometric characters of the larvae were measured: total length (TOL, distance from tip of snout to tip of tail); snout-vent length (SVL, distance from tip of snout to posterior edge of vent); head length (HDL, distance from jugular fold to snout tip); head width (HDW, maximum head width); snout length (SL, distance from tip of snout to the anterior corner of eye); eye diameter (ED, distance from the anterior corner to the posterior corner of the eye); interorbital distance (IOD, minimum distance between the eyes); internasal distance (IND, minimum distance between the external nares); trunk length (TRL, from gular fold of throat to anterior tip of vent); tail length (TAL, from anterior tip of cloaca to tip of tail); tail height (TH, maximum tail height); length of lower arm and hand (LAL, distance from the elbow to the distal end of the longest finger); and the length of hind leg (HLL, from groin to tip of the longest toe).

For morphometric analyses, in order to reduce the impact of allometry, the correct value from the ratio of each character to TOL was calculated and then was log-transformed. Mann-Whitney *U* tests were conducted to test the significance of differences on morphometric characters between the undescribed species, *T. anhuiensis*, *T. broadoridgus*, *T. dabienicus* and *T. wenxianensis*. The significance level was set at 0.05. Furthermore, principal component analyses (PCA) were conducted to highlight whether the different species were separated in morphometric space. Due to only the measurements TOL, SVL, HDL, HDW, TRL, SL, ED, IOD, TAL and TH of male *T. anhuiensis* being available from Qian *et al.* (2017), the morphometric analyses were conducted only based on these ten morphometric characters for PCA in male group. The analyses were carried out in R (R Development Core Team).

The undescribed species was clustered into the *T. wenxianensis* species group (Wang et al. 2018), and it was compared with the members of this group on morphology. Comparative morphological data were obtained from literature for *T. anhuiensis* (Qian et al., 2017), *T. asperrimus* (Unterstein, 1930), *T. broadoridgus* (Shen et al., 2012), *T. dabienicus* (Chen et al., 2010), *T. liuyangensis* (Yang et al., 2014), *T. lizhenchangi* (Hou et al., 2012), and *T. wenxianensis* (Fei et al., 1984).

2.4. Skull scanning Skulls of three male specimens (voucher numbers: CIBML20180427001, CIBML20180427002 and CIBML20180427004) and two female specimens (voucher numbers: CIBML20180427003 and CIBML20180427006) of the undescribed species were scanned in the high-resolution X-ray scanner (Quantum GX micro-CT Imaging System; PerkinElmer, Boston, MA, USA) in CIB, CAS. The specimens were scanned along the coronal axis at an image resolution of 2000 × 2000. Segmentation and three-dimensional reconstruction of the CT images were made using VG57 Studio Max 2.2 (Volume Graphics, Heidelberg, Germany).

3. Results

3.1. Phylogenetic analyses Aligned sequence matrix of 16S + ND2 genes contained 1540 bps. ML and BI analyses resulted in essentially identical topologies (Figure 2). The genus *T. sensu lato* was strongly supported as a monophyly. All samples of the undescribed species occurring from Maolan National Nature Reserve of Guizhou Province, China were strongly nested into one clade, which was sister to *T. broadoridgus*, and close to *T. wenxianensis*, *T. dabienicus* and *T. anhuiensis*.

Genetic distance on ND2 gene with uncorrected *p*-distance model between specimens of the undescribed species was less than 0.5%, much lower than interspecific genetic distances of the genus *T. sensu lato* (1.2%–14.3%; Table 2). Genetic distances between the undescribed species and its closely related species, *T. dabienicus*, *T. anhuiensis*, *T. broadoridgus* and *T. wenxianensis* were 2.8%–3.9% (Table 2), being higher than that between some substantial sister species, for example, *T. shanjing* vs. *T. verrucosus* (1.2%), *T. shanjing* vs. *T. pulcherrimus* (2.5%), *T. verrucosus* vs. *T. pulcherrimus* (2.1%), and *T. taliangensis* vs. *T. pseudoverrucosus* (2.7%). Genetic distance on 16S gene and 16S+ND2 data between the new species and *T. anhuiensis*, *T. broadoridgus*, *T. dabienicus* and *T. wenxianensis* are also in the same level, i.e., 0.8%–1.6% on 16S gene and 2.2%–2.9% on 16S+ND2 data (Table S2).

3.2. Morphological comparisons In PCA, for males, the total variation of the first two principal components was 75.3%, and for females was 52.3%. Both in males and females on the two-dimensional plots of PC1 vs. PC2, the undescribed species could be separated from its closely related species *T. anhuiensis*, *T. broadoridgus*, *T. dabienicus* and *T. wenxianensis* (Figure 3). The results of Mann-Whitney U tests indicated that in males, the undescribed species was significantly different from *T. anhuiensis*, *T. broadoridgus*, *T. dabienicus* and *T. wenxianensis* on a series of morphometric characters (all *P*-values < 0.05; Table 3). More detailed descriptions of the results from morphological comparisons between the undescribed species and its congeners were presented in the following sections for describing the new species.

3.3. Description of the new species

Tylototriton maolanensis sp. nov.

Holotype. Figures 4 A, 5A, 5B, 5I, 5K, 5L, 6. Male, CIBML20180427001, collected on 27 April 2018 by Shize LI from Maolan National Nature Reserve (25.307194° N, 107.948764° E, ca. 737 m a.s.l.) in Libo County, Guizhou Province, China.

Paratype. Five adult males (CIBML20180427002, CIBML20180427004, CIBML20180427005, CIBML20180427007 and CIBML20180427008), two females (CIBML20180427003 and CIBML20180427006) and one larva (CIBML2019015001) were collected on 27 April 2018 by Shize Li together with the holotype.

Diagnosis. *T. maolanensis* sp. nov. is assigned to the genus *T. sensu lato* based upon molecular phylogenetic analyses and the following morphological characters: presence of dorsal granules, dorsolateral bony ridges on the head, knob-like warts on dorsolateral body, and the absence of a quadrate spine.

T. maolanensis sp. nov. could be distinguished from its congeners by a combination of the following characters: (1) large body size (SVL 76.8–85.2 mm in male and 76.3–87.4 mm in female); (2) head length longer than wide; (3) snout truncate in dorsal view; (4) the tail length longer than the snout-vent length in males; (5) the distal digit ends, ventral digits, peripheral area of cloaca and the tail's lower margin orange; (6) relative length of toes III > IV > II > I > V; (7) the distal tips of the limbs greatly overlapping when the fore and hind limbs being pressed along the trunk; (8) fingertips reaching to the level beyond the snout while the forelimbs being stretched forward.

Description of holotype. Measurements in mm. Figures 4 A, 5 A, 5B, 5I, 5K, 5L. SVL 80.8; TOL 165.2; head longer

Table 2 Uncorrected *p*-distances between the *Tylototriton sensu lato* species based on the ND2 gene.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1 <i>Tylototriton maolanensis</i> sp. nov.																									
2 <i>Tylototriton broadoridgus</i>	0.028																								
3 <i>Tylototriton dabienicus</i>	0.034	0.033																							
4 <i>Tylototriton anhuiensis</i>	0.032	0.035	0.037																						
5 <i>Tylototriton wenxianensis</i>	0.039	0.043	0.047	0.040																					
6 <i>Tylototriton lizhanchang</i>	0.080	0.084	0.086	0.082	0.079																				
7 <i>Tylototriton liuyangensis</i>	0.071	0.071	0.072	0.071	0.070	0.072																			
8 <i>Tylototriton hainanensis</i>	0.082	0.076	0.087	0.078	0.087	0.087	0.077																		
9 <i>Tylototriton notialis</i>	0.080	0.079	0.086	0.081	0.086	0.096	0.085	0.046																	
10 <i>Tylototriton asperimus</i>	0.084	0.085	0.089	0.082	0.087	0.104	0.087	0.050	0.053																
11 <i>Tylototriton zieglerei</i>	0.083	0.079	0.087	0.080	0.088	0.101	0.084	0.044	0.048	0.044															
12 <i>Tylototriton vietnamensis</i>	0.109	0.109	0.108	0.107	0.103	0.116	0.107	0.107	0.118	0.108	0.112														
13 <i>Tylototriton panhai</i>	0.099	0.093	0.093	0.093	0.101	0.097	0.093	0.096	0.102	0.110	0.099	0.111													
14 <i>Tylototriton shanjing</i>	0.099	0.103	0.108	0.103	0.099	0.116	0.105	0.103	0.110	0.114	0.112	0.123	0.126												
15 <i>Tylototriton verrucosus</i>	0.099	0.103	0.108	0.105	0.097	0.115	0.103	0.103	0.110	0.115	0.112	0.121	0.125	0.012											
16 <i>Tylototriton pulcherrimus</i>	0.095	0.099	0.103	0.098	0.091	0.108	0.099	0.095	0.103	0.109	0.104	0.118	0.120	0.025	0.021										
17 <i>Tylototriton podichthys</i>	0.098	0.100	0.106	0.097	0.096	0.112	0.102	0.102	0.107	0.108	0.107	0.130	0.122	0.043	0.041	0.037									
18 <i>Tylototriton uyanoi</i>	0.124	0.128	0.131	0.126	0.125	0.129	0.126	0.125	0.127	0.129	0.133	0.148	0.143	0.073	0.073	0.068	0.082								
19 <i>Tylototriton anguliceps</i>	0.107	0.109	0.119	0.107	0.107	0.123	0.102	0.100	0.107	0.113	0.108	0.131	0.129	0.044	0.044	0.040	0.053	0.073							
20 <i>Tylototriton yangi</i>	0.095	0.101	0.108	0.100	0.097	0.110	0.095	0.096	0.103	0.102	0.101	0.121	0.124	0.044	0.040	0.038	0.051	0.075	0.042						
21 <i>Tylototriton shanorum</i>	0.102	0.102	0.109	0.107	0.111	0.118	0.103	0.098	0.109	0.113	0.109	0.122	0.123	0.066	0.062	0.062	0.074	0.091	0.067	0.064					
22 <i>Tylototriton ngarsuensis</i>	0.115	0.116	0.123	0.119	0.120	0.129	0.115	0.110	0.120	0.123	0.120	0.130	0.132	0.073	0.070	0.070	0.083	0.101	0.077	0.073	0.018				
23 <i>Tylototriton himalayanus</i>	0.104	0.104	0.110	0.107	0.105	0.114	0.101	0.098	0.105	0.115	0.109	0.128	0.122	0.063	0.065	0.062	0.068	0.085	0.069	0.066	0.050	0.065			
24 <i>Tylototriton kweichowensis</i>	0.095	0.090	0.103	0.097	0.098	0.107	0.095	0.086	0.100	0.102	0.092	0.120	0.106	0.060	0.057	0.054	0.061	0.080	0.062	0.062	0.059	0.070	0.053		
25 <i>Tylototriton taliangensis</i>	0.088	0.093	0.091	0.089	0.086	0.095	0.090	0.086	0.091	0.093	0.095	0.112	0.104	0.074	0.074	0.073	0.077	0.100	0.084	0.078	0.081	0.091	0.075	0.065	
26 <i>Tylototriton pseudoverrucosus</i>	0.091	0.093	0.095	0.093	0.093	0.100	0.091	0.085	0.089	0.097	0.093	0.117	0.103	0.077	0.075	0.067	0.073	0.100	0.085	0.074	0.079	0.087	0.071	0.060	0.027

than wide (HDL/HDW = 1.12); head slightly concave on the top; snout is nearly square, extending beyond the lower lip; naris nearly snout; snout truncate in dorsal view; the supratemporal ridges on the head are long,

steep and notable, extending from the dorsal region of the rostral side, and through the interior side of the upper eyelid to the occiput; a pair of short and protruding ridges on middle of supratemporal ridges; two triangular bony

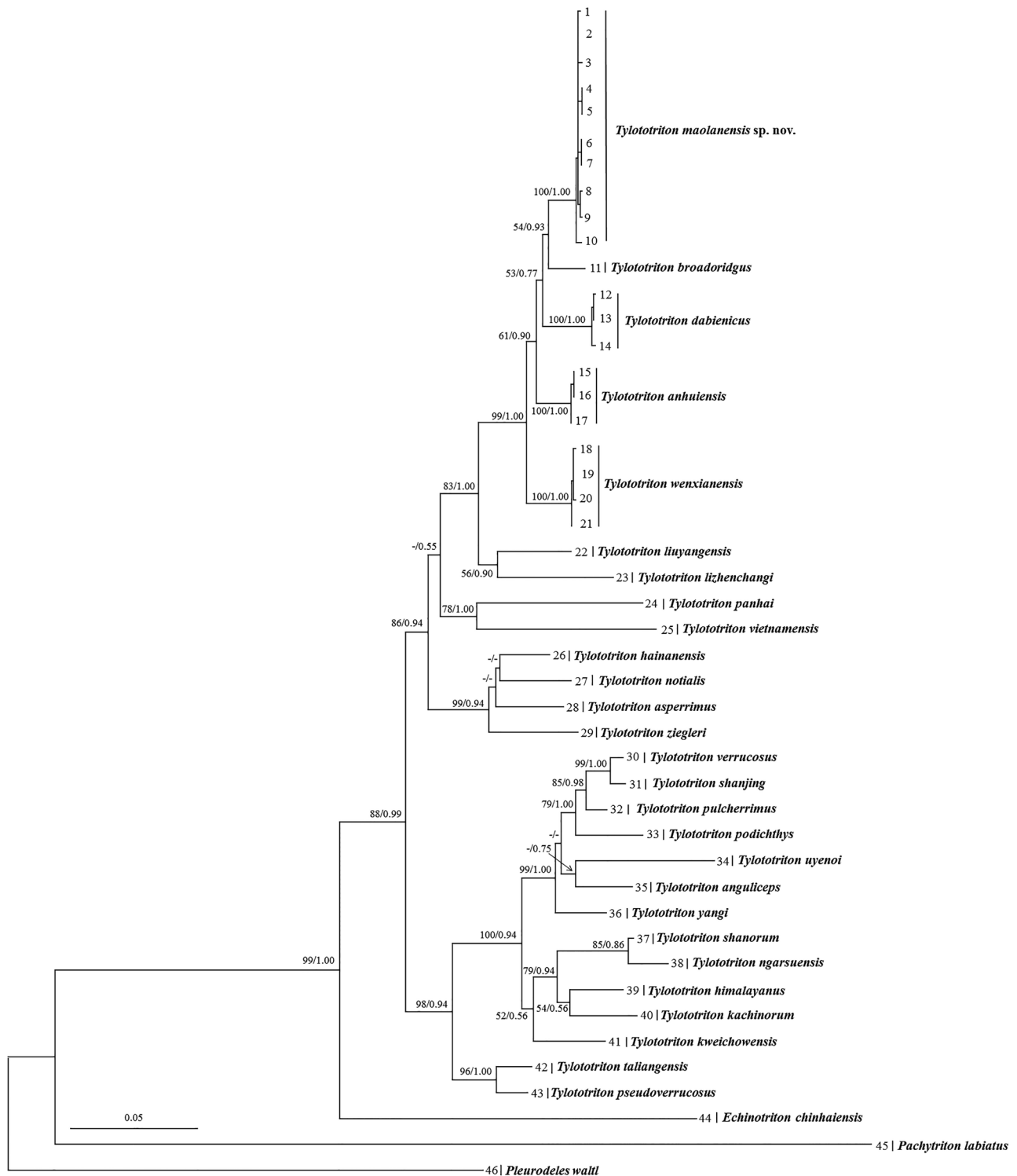


Figure 2 Maximum likelihood (ML) tree reconstructed based on the mitochondrial 16S and ND2 gene sequences. Bootstrap supports (BS) /Bayesian posterior probabilities (BPP) were labeled beside nodes. Information of samples 1–46 refer to Table 1.

ridges on the occiput point laterally edge, distinctly being not connected with the dorsal ridge of body; two bony ridges on the dorsal head surface form a “V” shape and disconnected with the dorsal ridge of body; inter-nasal space is smaller than the inter-orbital space; eyes protrude from the dorsolateral portion of the head; the oral fissure is flat; the joint of jaw articulation lies posterior to the caudal margin of the eyes; fine teeth present on the edge of jaw, vomerine teeth long and prominent, form a “^” shape which separated from each other at the tip of the “^” shaped; tongue oval and nearly entirely fixed at bottom but free at both lateral edges; neck is rounded and thick, with distinct neck groove.

Body is stout; two sides of the ridge are slightly concave. Each lateral corner of the dorsal ridge consists of 17 knob-like dorsal warts, and fine transverse striae present between every two knob-like dorsal warts.

Four limbs are relatively slender, and hind limbs are slightly longer than forelimbs; the distal tips of limbs greatly overlapping when fore and hind limbs are pressed along the trunk; fingertips are reaching to the level beyond the snout while the forelimbs are stretched forward; relative fingers length is $\text{III} > \text{II} > \text{IV} > \text{I}$, and relative toes length is $\text{III} > \text{IV} > \text{II} > \text{I} > \text{V}$; fingers and digits are with none webbed.

The tail length is longer than the snout-vent length; the tail is notably compressed laterally; the dorsal fin fold of the tail, starting from the tail base, distinctly thin and high; while the ventral fin fold of tail, starting from posterior to the cloaca, is thick and short; the tail height is greater than the width at the tail base, and the distal tail tip is rounded; the cloaca is long and narrow, and the cloacal region is slightly bulbous.

The skin is extremely rough, and body covered with tubercles and warts; the labial margin, distal limbs, ventral limbs and the ventral edge of the tail are smooth; the dorsal ridge, running along the middle of the dorsum and extending from the neck to the base of the tail, is rough and relatively narrow; each lateral corner of the dorsal ridge consists of a row of rough knob-like dorsal warts; on the lateral dorsum of the body, tubercles and warts are big, appearing to form lines that extend from the shoulder to the base of the tail; the ventral tubercles and warts are relatively flat and smaller.

Color in life. Figure 5 A, B, I, K, L. In life, the specimen black or blackish-brown, while the ventral color little lighter; the distal digit ends, ventral digits, the peripheral area of cloaca and the ventral edge of tail are orange; the orange region between the ventral edge of the tail and the peripheral area of the cloaca is connected.

Color in preservative. Figure 4 A. The specimen in preservative is black and the ventral color is blackish-brown. The orange coloration of the distal digit ends, ventral digits, the peripheral area of the cloaca and the ventral edge of the tail fades to lacte.

Variation. A large proportion of specimens were similar in morphology with the holotype, but some individuals are different. In female individuals the tail length is shorter than the snout-vent length; in some individuals the knob-like dorsal warts on lateral corner of the dorsal ridge are not black but with orange slightly, and in some individuals the knob-like dorsal warts on lateral corner of the dorsal ridge are 13, 15, 16 or 17 (Figures 5 C–5 F, 5 J)

Secondary sexual characteristics. The female cloacal hole is short and its inner cloacal wall has no papilla

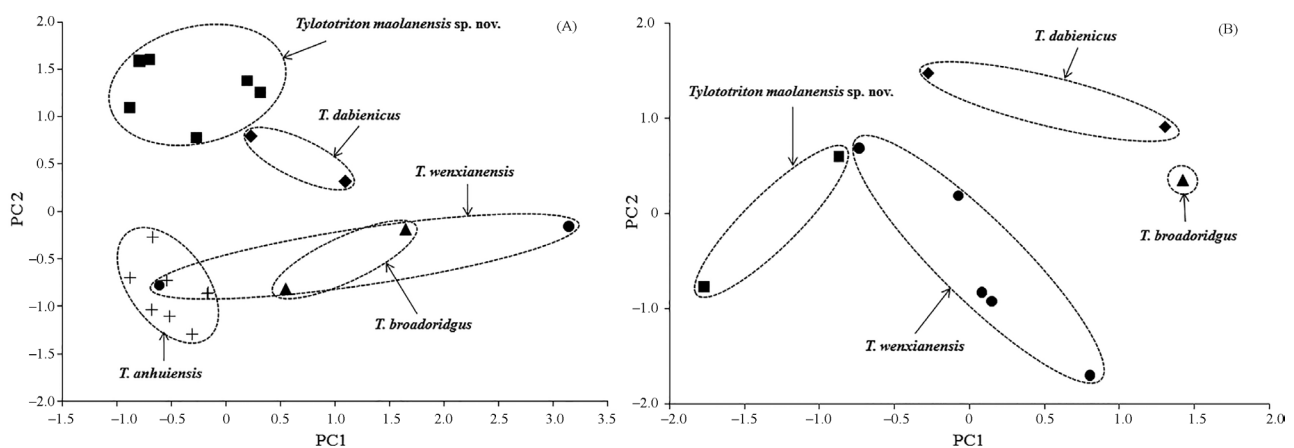


Figure 3 Plots of principal component analyses for *Tylototriton maolanensis* sp. nov. and its relatives. A, male. B, female. PC1, the first principal component; PC2, the second principal component.

Table 3 Morphometric comparisons between *Tylototriton maolanensis* sp. nov. (TM), *T. anhuiensis* (TA), *T. broadoridgus* (TB), *T. dabienicus* (TD) and *T. wenxianensis* (TW). P-value was resulted from Mann-Whitney U test.

Character	Mean ± SD for male										Mean ± SD for female										P-value													
	TM (n = 6)					TB (n = 2)					TD (n = 2)					TW (n = 2)					TA (n = 8)					TM (n = 5)					Male		Female	
	TM	TB	TD	TW	TA	TM	TB	TD	TW	TA	TM	TB	TD	TW	TA	TM	TB	TD	TW	TA	TM	TB	TD	TW	TA	TM vs. TB	TM vs. TD	TM vs. TW	TM vs. TA	TM vs. TB	TM vs. TD	TM vs. TW	TM vs. TA	
TOL	163.9 ± 7.7	124.2 ± 0.6	147.9 ± 15.6	119.9 ± 4.0	127.9 ± 5.9	156.6 ± 19.7	138.0 ± 0.1	134.6 ± 7.4			80.8 ± 3.7	67.4 ± 1.8	70.7 ± 4.7	66.0 ± 7.1	68.6 ± 2.5	81.9 ± 7.8	73.6 ± 5.0	72.5 ± 4.3			0.046	0.182	0.046	0.002	0.002	0.121	0.121	0.002	0.002	0.121	0.121	0.121	0.121	
SVL	20.7 ± 0.8	18.9 ± 0.4	20.3 ± 0.8	18.8 ± 1.6	15.5 ± 0.9	21.1 ± 1.2	19.4 ± 0.8	19.3 ± 1.0			17.5 ± 1.0	15.2 ± 0.8	15.2 ± 0.4	15.6 ± 0.9	14.0 ± 0.6	18.9 ± 2.0	14.9 ± 0.0	16.7 ± 1.1			0.046	0.182	0.046	0.046	0.046	0.121	0.121	0.046	0.046	0.121	0.121	0.121	0.121	
HDW	63.9 ± 3.7	54.2 ± 0.6	54.6 ± 3.7	51.9 ± 2.0	54.4 ± 2.2	64.9 ± 8.9	54.0 ± 1.4	58.2 ± 4.6			6.9 ± 0.4	5.8 ± 1.0	6.1 ± 0.3	5.7 ± 0.3	3.4 ± 0.3	6.2 ± 0.1	6.2 ± 0.2	5.9 ± 0.2			0.046	0.182	0.046	0.003	0.003	0.121	0.121	0.003	0.003	0.121	0.121	0.121	0.121	
TRL	3.5 ± 0.2	4.2 ± 0.3	3.8 ± 0.2	3.7 ± 0.0	3.6 ± 0.3	3.5 ± 0.7	3.9 ± 0.1	3.6 ± 0.4			9.0 ± 0.6	7.9 ± 0.0	8.2 ± 0.2	8.4 ± 0.0	/	9.6 ± 0.9	8.6 ± 0.2	8.5 ± 0.4			0.046	0.182	0.046	0.002	0.002	0.121	0.121	0.002	0.002	0.121	0.121	0.121	0.121	
ED	13.4 ± 1.1	11.8 ± 0.5	11.8 ± 0.2	12.2 ± 0.8	/	13.5 ± 1.5	12.6 ± 0.1	12.4 ± 0.4			2.2 ± 0.4	1.7 ± 0.1	1.8 ± 0.4	1.7 ± 0.1	/	2.0 ± 0.5	1.9 ± 0.1	1.9 ± 0.2			0.046	0.182	0.046	/	/	0.121	0.121	/	/	0.121	0.121	0.121	0.121	
UAE	8.3 ± 0.4	7.9 ± 0.1	7.8 ± 0.4	8.6 ± 0.2	7.1 ± 0.5	8.4 ± 0.6	8.2 ± 0.4	8.4 ± 0.5			5.7 ± 0.5	4.7 ± 0.8	4.9 ± 0.1	4.8 ± 0.2	/	6.4 ± 0.5	5.2 ± 0.2	4.8 ± 0.4			0.046	0.182	0.046	0.053	0.053	0.121	0.121	0.053	0.053	0.121	0.121	0.121	0.121	
IOD	10.2 ± 0.6	8.7 ± 0.0	9.7 ± 0.1	10.0 ± 1.4	/	9.8 ± 0.8	8.8 ± 0.0	8.8 ± 0.8			9.3 ± 0.5	6.0 ± 0.2	7.2 ± 0.3	6.8 ± 0.8	/	9.9 ± 1.3	7.0 ± 0.7	7.7 ± 0.7			0.046	0.182	0.046	/	/	0.121	0.121	/	/	0.121	0.121	0.121	0.121	
HL	9.3 ± 0.5	6.0 ± 0.2	7.2 ± 0.3	6.8 ± 0.8	/	9.9 ± 1.3	7.0 ± 0.7	7.7 ± 0.7			5.7 ± 0.7	4.7 ± 0.1	5.6 ± 0.4	5.1 ± 0.2	/	6.1 ± 0.6	5.5 ± 1.1	4.7 ± 0.7			0.046	0.182	0.046	/	/	0.121	0.121	/	/	0.121	0.121	0.121	0.121	
LLA	10.5 ± 0.7	11.0 ± 0.1	12.6 ± 0.8	11.7 ± 0.4	/	11.0 ± 0.8	11.6 ± 0.1	11.8 ± 0.7			9.1 ± 0.7	7.6 ± 1.1	7.2 ± 0.4	7.6 ± 0.3	/	9.5 ± 0.4	8.1 ± 1.1	7.9 ± 0.4			0.046	0.182	0.046	/	/	0.121	0.121	/	/	0.121	0.121	0.121	0.121	
FIHL	7.3 ± 0.5	5.7 ± 0.7	5.4 ± 0.6	6.1 ± 0.6	/	8.4 ± 1.6	7.8 ± 2.4	5.8 ± 0.4			7.3 ± 0.5	5.7 ± 0.7	5.4 ± 0.6	6.1 ± 0.6	/	8.4 ± 1.6	7.8 ± 2.4	5.8 ± 0.4			0.046	0.182	0.046	0.053	0.053	0.121	0.121	0.053	0.053	0.121	0.121	0.121	0.121	
THL	85.4 ± 5.0	57.0 ± 1.4	72.2 ± 3.8	53.6 ± 6.8	59.4 ± 3.9	75.6 ± 12.1	68.1 ± 0.3	65.9 ± 3.5			7.8 ± 1.0	7.4 ± 0.8	7.9 ± 0.2	6.7 ± 2.4	7.4 ± 0.7	8.9 ± 1.9	7.6 ± 1.1	8.1 ± 1.2			0.046	0.182	0.046	0.002	0.002	0.439	0.439	0.002	0.002	0.439	0.439	0.439	0.439	
TH	7.8 ± 1.0	7.4 ± 0.8	7.9 ± 0.2	6.7 ± 2.4	7.4 ± 0.7	8.9 ± 1.9	7.6 ± 1.1	8.1 ± 1.2													0.046	0.182	0.046	0.02	0.02	1	1	0.02	0.02	1	1	0.02	0.02	

(Figure 5 I). The male has papilla on its inner cloacal wall and its cloacal orifice long slit (Figure 5 J).

Skull. The skull morphology of the five scanned specimens were almost identical, and thus, one representative (voucher number: CIBML20180427002) was presented (Figure 6) and described as following. Skull wider than long, equipped with numerous sculpture-shaped ridges dorsally. Nasal connects with one another along the midline, with the maxilla laterally, with the premaxilla anteriorly, and with the prefrontal and the frontal posteriorly. The nasal process is short and far away from the frontal. Both the septomaxilla and the lacrimal are absent. The frontal is obviously larger than the parietal. The squamosal is enlarged. The frontosquamosal arch is robust. The pterygoid is not directly meet with the maxilla. The maxilla is long, its anterior margin contacts with the premaxilla, and its posterior end contacts with the quadrate posteriorly. The premaxilla and the vomer form a fontanelle. The vomer is large and gradually narrowed from anteriorly to posteriorly. The vomerine teeth series are arranged in inverted V shape. The parasphenoid wedges between the vomers.

Larva. A larva was collected from the same pond of holotype on 27 April, 2018 (Figure 7). Measurements in mm. TOL 55.2, SVL 31.8, HDL14.2, HDW7.6, TRL23.3, LAL7.4, HLL10.2, ED2.1, TAL23.8, TH4.3, IND2.4, IOD3.1, and SL3.2. Body slender. The forelimbs and hindlimbs clearly fully grown up. Head longer than wide, eyes relatively large on the flank and three pairs of external gills having obtuse anterior ends, while the body and tail being laterally compressed. Skin smooth, and except the ventral side of the tail, fingers and toes saffron yellow, body black-brown. Costal grooves for muscles of larvae distinctly. The dorsal fin fold comparatively tall and rises from the region between the posterior head and anterior body. The short and thick ventral fin fold of the tail extends from the cloaca to the end of the tail.

Morphological comparisons. *T. maolanensis* sp. nov. had been identified as *T. asperimus* (Wu *et al.*, 1986; Fei *et al.*, 2012; Gu *et al.*, 2012), but molecular phylogenetic analyses revealed that this new species was genetically closer to *T. anhuiensis*, *T. broadoridgus*, *T. dabienicus*, *T. wenxianensis*, *T. liuyangensis* and *T. lizhenchangi*. The new species can be distinguished from these closely-related species by a series of morphological characters (Figure 4; Table 3) as follows.

T. maolanensis sp. nov. differs from *T. asperimus* by tail length longer than snout-vent length in males (vs. tail length shorter than snout-vent length in males); the distal tip of limbs greatly overlapping when the fore and hind

limbs pressed along the trunk (vs. slightly overlapping, meeting or not meeting); fingertips reaching to the level beyond the snout while the forelimbs stretched forward (vs. just reaching to the nostril or eye).

T. maolanensis **sp. nov.** differs from *T. anhuiensis* by tail length longer than snout-vent length in males (vs. snout-vent length longer than tail length); the relative toes length $I > V$ (vs. $V > I$); the distal tips of the limbs greatly overlapping when the fore and hind limbs pressed along the trunk (vs. slightly overlapping); having significantly longer TOL in males; having significantly higher ratios of ED, SVL, TRL, SL, TAL and TH to TOL in males; the

transverse striae present between every two knob-like dorsal warts (vs. every two knob-like dorsal warts closely arranged); dorsolateral bony ridge on head steep, long, narrow and prominent (vs. dorsolateral bony ridge on head slightly prominent, gentle and wide); snout truncate in dorsal view (vs. snout obtusely rounded in dorsal view); and having long and strong vomerine tooth (vs. vomerine teeth short).

T. maolanensis **sp. nov.** differs from *T. dabienicus* by tail length longer than snout-vent length in males (vs. snout-vent length longer than tail length); the relative toes length $I > V$ (vs. $V > I$); the distal tips of the limbs greatly

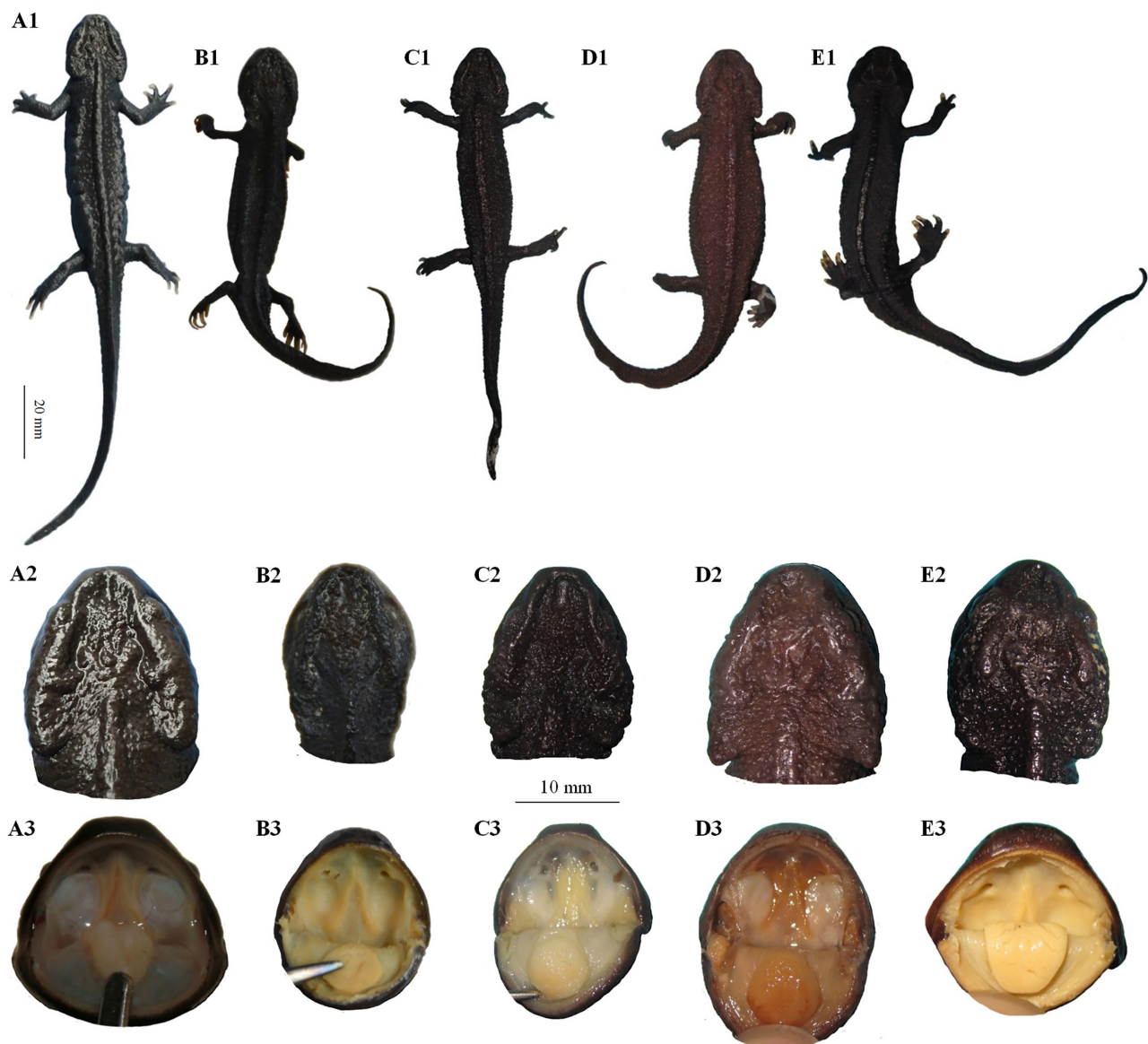


Figure 4 Photos of the holotype specimen of *Tylototriton maolanensis* sp. nov. and topotype specimens of its closely related species. A, holotype specimen CIBML20180427001 of *Tylototriton maolanensis* **sp. nov.** B, topotype specimen AHU-16-EE-001 of *T. anhuiensis*. C, topotype specimen CIBSZ20120620026 of *T. broadoridgus*. D, topotype specimen CIB8042905 of *T. dabienicus*. E, specimen CIB200811CD03 of *T. wenxianensis*. A1–E1, dorsal view of whole body. A2–E2, dorsal view of head. A3–E3, view of oral cavity.

overlapping when the fore and hind limbs pressed along the trunk (vs. slightly meeting or not meeting); fingertips reaching to the level beyond the snout while the forelimbs

stretched forward (vs. reaching to the eye); having significantly higher ratios of ED, TLH, TL and TAL to TOL in males; by dorsolateral bony ridge on head steep,



Figure 5 Photos showing color variation in *T. ylotriton maolanensis* sp. nov. in life. A and B, dorsal and ventral view of the holotype CIBML20180427001. C and D, dorsal and ventral view of the female paratype CIBML20180427003. E–H, dorsolateral view of the female paratype CIBML20180427006, and male paratypes CIBML20180427002, CIBML20180427004, and CIBML20180427008. I and J, cloaca of the holotype CIBML20180427001 and paratype CIBML20180427003. K and L, the ventral view of the hand and foot of the holotype CIBML20180427001.

long, narrow and prominent (vs. prominent but gentle and wild); by snout truncate in dorsal view (vs. snout obtusely rounded in dorsal view); by the bony ridges on the head extending from the dorsal region of the rostral side, and through the interior side of the upper eyelid to the occiput (vs. extending from the dorsal region of the rostral side to the posterior of orbit); by having a bigger angle formed by ends of vomerine teeth (vs. the angle smaller); by the separated tip of “ \wedge ” shaped vomerine teeth (vs. tip of “ \wedge ” shaped vomerine teeth connected).

T. maolanensis **sp. nov.** differs from *T. wenxianensis* by having a longer body length in males (minimum total length > 151 mm vs. maximum total length < 134 mm in the latter); head length longer than wide (vs. length equal to wide); tail length longer than snout-vent length in males (vs. snout-vent length longer than tail length); the relative toes length $I > V$ (vs. $V > I$); the distal tips of the limbs greatly overlapping when the fore and hind limbs pressed along the trunk (vs. slightly meeting or slightly overlapping); fingertips reaching to the level beyond the snout while the forelimbs stretched forward (vs. reaching to the nostril); having significantly higher ratios of TOL and having significantly lower ratios of HDL, HDW, TRL, SL, ED, IFE, IAE, IOD, IND, HL, TLH, TL and TAL to TOT in males; by snout truncate in dorsal view (vs. snout obtusely rounded in dorsal view); by dorsolateral bony ridge on head steep, long, narrow and prominent (vs. prominent but gentle and wild); by the separated tip of “ \wedge ” shaped vomerine teeth (vs. tip of “ \wedge ” shaped vomerine teeth connected).

T. maolanensis **sp. nov.** differs from *T. broadoridgus* by

having a longer body length in males (minimum total length > 151 mm vs. maximum total length < 141 mm in the latter); tail length longer than snout-vent length in males (vs. snout-vent length longer than tail length); the relative toes length $I > V$ (vs. $V > I$); the distal tips of the limbs greatly overlapping when the fore and hind limbs pressed along the trunk (vs. slightly overlapping or just meeting); having significantly higher ratios of TOL, and significantly higher ratios of SVL, HDL, HDW, TRL, ED, IFE, IAE, IOD, LLA, TLH, TAL and TH to TOL; by dorsolateral bony ridge on head steep, long, narrow and prominent (vs. prominent but gentle); by having a bigger angle formed by ends of vomerine teeth (vs. the angle smaller).

T. maolanensis **sp. nov.** differs from *T. liuyangensis* by having a longer body length in males (minimum total length > 151 mm vs. maximum total length < 147 mm in the latter), tail length longer than snout-vent length in males (vs. shorter), the relative toes lengths $I > V$ (vs. $V > I$), the distal tip of limbs greatly overlapping when the fore and hind limbs pressed along the trunk (vs. slightly overlapping, meeting or not meeting), the distal tip of limbs greatly overlapping when the fore and hind limbs pressed along the trunk (vs. slightly overlapping, meeting or not meeting).

T. maolanensis **sp. nov.** differs from *T. lizhenchangii* by head length longer than wide (vs. wider than long or equal in the latter), the relative toes lengths $I > V$ (vs. $V > I$).

Ecology. *T. maolanensis* **sp. nov.** is currently known from Maolan National Nature Reserve (25.155°–25.347° N,

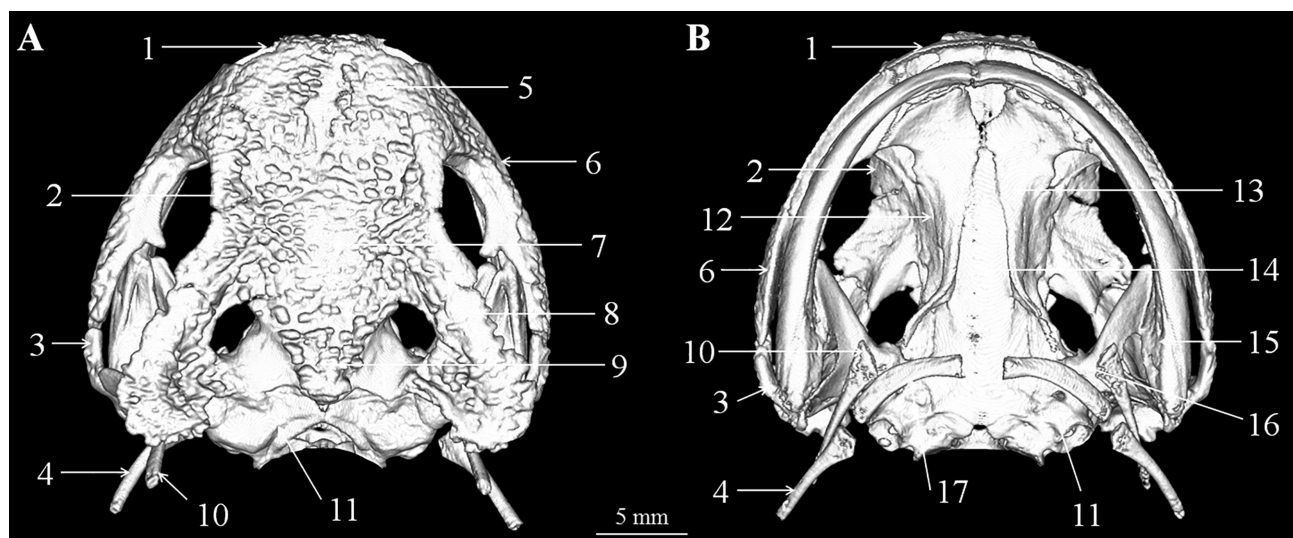


Figure 6 Skull of the holotype specimen CIBML20180427001 of *Tylotriton maolanensis* sp. nov. A, dorsal view. B, ventral view. (1) premaxilla; (2) prefrontal; (3) quadrate; (4) ceratobranchial 1; (5) nasal; (6) maxilla; (7) frontal; (8) squamosal; (9) parietal; (10) ceratohyal; (11) prootic-exoccipital complex; (12) orbitosphenoid; (13) vomer; (14) parasphenoid; (15) prearticular-angular; (16) pterygoid; (17) hypobranchial 1.



Figure 7 Photos of larva CIBML2019015001 of *Tylototriton maolanensis* **sp. nov.** in life. A, dorsal view. B, lateral view. C, ventral view.

107.869°–108.761° E) in Libo County, Guizhou Province, China. It inhabited in the puddles on a hillside or at the foot of a hill (Figure 8), at elevations of about 737 m a. s. l. Two sympatric amphibian species, *Microhyla heymonsi* Vogt, 1911 and *Hylarana latouchii* Boulenger, 1920, were found in the type locality.

Etymology. The specific name *maolanensis* is a Latinize toponymic adjective that refers to Maolan National Nature Reserve, Libo County, Guizhou Province, China, where the new species was firstly found. For the common name, we suggest Maolan Knobby Newt (English) and Mao Lan You Yuan (茂兰疣螈, Chinese).

4. Discussion

Most cryptic congeners in the genus *T. sensu lato* are

difficult to be distinguished from each other due to the superficial similarities in morphology. This resulted in considerable challenges in field identification, which in turn cause ambiguities in taxonomy arrangement (Fei and Ye, 2016; Fei *et al.*, 2006, 2012). *T. maolanensis* **sp. nov.** had been initially identified as *T. asperrimus* (Wu *et al.*, 1986; Gu *et al.*, 2012; Fei *et al.*, 2012). In this study, phylogenetic analyses suggested that the new species was separated from its congeners. Genetic distance between the new species and its closely-related species (*T. dabienicus*, *T. anhuiensis* and *T. broadoridgus*) were much higher than that between many sister species in *T. sensu lato*. Indeed, there were some subtle morphological differences between the new species and its congeners with comparisons. Hence, all evidences supported that *T. maolanensis* **sp. nov.** is a valid species. Wang *et al.* (2018) indicated that the distributional range of *T. wenxianensis* species group (containing *T. anhuiensis*, *T. broadoridgus*, *T. dabienicus*, *T. wenxianensis*, *T. liuyangensis*, *T. lizhenchangi* and *T. maolanensis* **sp. nov.**) was basically in the north of Nanling Mountain series, and the *T. asperrimus* species group was distributed in the south of Nanling Mountain series. Maolan National Nature Reserve is located in the boundary of them. However, in our surveys in recent many years in Maolan National Nature Reserve, we did not find individuals of *T. asperrimus* species group. Of course, we could not still exclude the possibility of the distribution of the *T. asperrimus* species group in Maolan, and deep field surveys in this area and/or adjacent areas are needed.

Tylototriton newts were indicated to be poor dispersers and highly associated with specific habitat requirements for breeding and larval development (Zamudio and

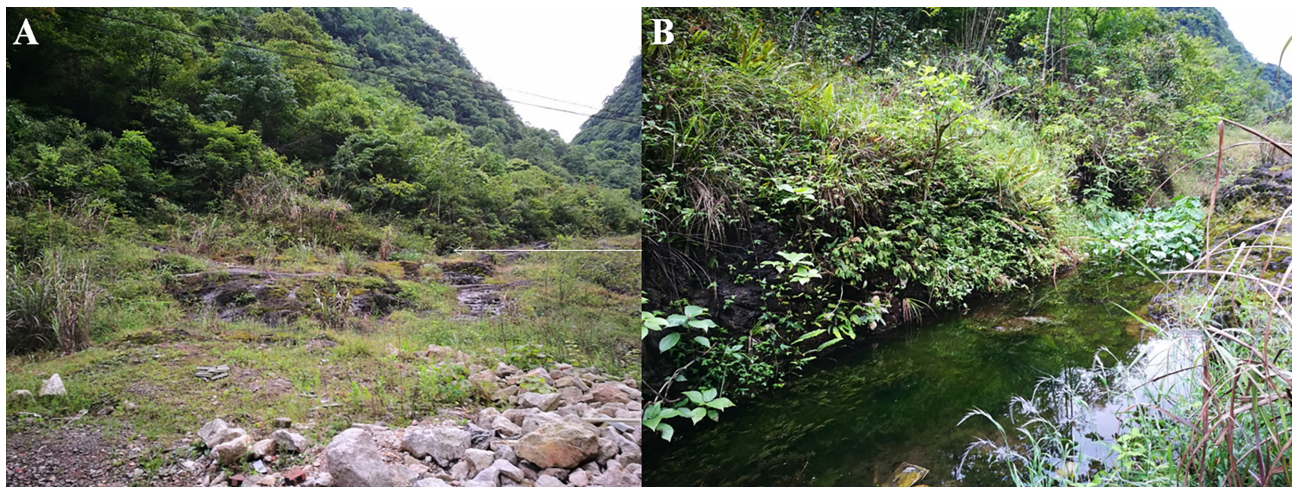


Figure 8 Habitats of *Tylototriton maolanensis* **sp. nov.** in the type locality, Maolan National Nature Reserve, Libo County, Guizhou Province, China. A, landscape. B, micro-habitat.

Wieczorek, 2007). In *T. wenxianensis* species group, except *T. wenxianensis*, each species (*T. anhuiensis*, *T. broadoridgus*, *T. dabienicus*, *T. liuyangensis*, *T. lizhenchangi* and *T. maolanensis* **sp. nov.**) has very a narrow distribution, and all of them are indicated to be separated (Wang *et al.* 2018). This indicated that local adaptation might impede the gene flow between them, and would cause great differentiation of species finally resulting in the formation of the new species (Eckert *et al.*, 2008).

Currently, to our knowledge, *T. maolanensis* **sp. nov.** live in the pond with broad-leaved forests or on the mountainside of Maolan National Nature Reserve. Thus, it is likely that other populations of *T. maolanensis* **sp. nov.** may be discovered in the nearby areas such as Mulun National Nature Reserve. We need to conduct deep surveys for investigate its distribution and population status because of increasing human activities and climate changes.

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Species Name	Voucher Number	Sex	Locality	TOL	SVL	HDL	HDW	TRL	SL	ED	IFE	IAE	UEW	IND	IOD	HL	LLA	FIHL	TLH	TL	TTHL	TAL	TH
<i>Tylosaurion maolanensis</i> sp. nov.	CIBM120180427003	Female	Libo Co, Guizhou Province, China	170.5	87.4	21.8	20.3	71.2	6.3	4.0	10.2	14.5	2.4	6.7	8.8	10.4	10.8	6.5	11.5	9.8	6.9	84.1	10.2
<i>Tylosaurion maolanensis</i> sp. nov.	CIBM120180427006	Female	Libo Co, Guizhou Province, China	142.7	76.3	20.1	17.5	58.6	6.2	3.0	8.9	12.4	1.7	6.0	7.9	9.2	9.0	5.7	10.4	9.2	7.9	67.0	7.5
<i>Tylosaurion maolanensis</i> sp. nov.	CIBM120180427007	Male	Libo Co, Guizhou Province, China	151.0	76.8	20.0	16.5	60.0	6.4	3.6	8.2	11.8	2.3	5.7	8.0	9.3	9.4	4.6	10.1	8.2	6.9	77.1	7.4
<i>Tylosaurion maolanensis</i> sp. nov.	CIBM120180427001	Male	Libo Co, Guizhou Province, China	165.2	80.8	21.4	19.1	62.2	7.2	3.7	9.5	14.8	2.6	6.0	8.4	10.0	9.3	5.3	11.1	8.7	7.9	85.2	9.8
<i>Tylosaurion maolanensis</i> sp. nov.	CIBM120180427005	Male	Libo Co, Guizhou Province, China	169.0	85.2	21.3	18.2	67.0	7.4	3.2	9.5	14.2	2.4	6.3	8.6	10.4	10.0	5.9	11.4	9.9	6.9	87.0	7.8
<i>Tylosaurion maolanensis</i> sp. nov.	CIBM120180427002	Male	Libo Co, Guizhou Province, China	167.6	79.6	20.0	17.2	61.8	6.8	3.2	8.6	13.2	2.4	5.2	7.7	10.4	9.4	5.6	10.4	9.1	7.3	90.5	6.9
<i>Tylosaurion maolanensis</i> sp. nov.	CIBM120180427008	Male	Libo Co, Guizhou Province, China	158.8	77.1	21.6	17.0	62.4	7.1	3.3	9.7	13.6	1.8	6.0	8.2	11.2	8.8	6.6	10.2	9.8	7.2	82.8	7.3
<i>Tylosaurion maolanensis</i> sp. nov.	CIBM120180427004	Male	Libo Co, Guizhou Province, China	172.0	85.2	20.1	17.1	69.7	6.3	3.7	8.6	13.0	1.6	5.0	8.8	10.0	8.8	6.0	9.6	9.1	0.0	90.0	7.4
<i>Tylosaurion broadrigus</i>	CIBSZ20120620023	Female	Sangzhi Co, Hunan Province, China	124.6	66.1	19.8	15.4	50.5	5.5	4.0	8.6	12.6	2.1	4.8	8.1	9.4	5.4	4.6	11.0	7.9	6.1	60.8	8.3
<i>Tylosaurion broadrigus</i>	CIB8080721A7	Male	Sangzhi Co, Hunan Province, China	123.7	68.7	18.6	14.7	54.6	5.2	4.4	7.9	11.5	1.6	4.1	8.0	8.7	5.8	4.6	11.1	6.8	5.2	58.0	6.8
<i>Tylosaurion broadrigus</i>	CIBSZ20120620026	Male	Sangzhi Co, Hunan Province, China	124.6	66.1	19.2	15.8	53.7	6.5	3.9	7.9	12.2	1.8	5.3	7.8	8.7	6.1	4.8	10.9	8.4	6.2	56.0	8.0
<i>Tylosaurion dahicus</i>	CIB8042906	Female	Shangcheng Co, Anhui Prov., China	138.6	77.2	19.9	14.9	55.0	6.4	4.0	8.5	12.6	2.0	5.3	7.9	8.8	7.5	6.3	11.6	7.3	6.1	67.9	6.8
<i>Tylosaurion dahicus</i>	CIB8042907	Female	Shangcheng Co, Anhui Prov., China	138.4	70.1	18.8	14.9	53.0	6.1	3.8	8.8	12.5	1.9	5.0	8.4	8.8	6.5	4.7	11.7	8.9	9.5	68.3	8.4
<i>Tylosaurion dahicus</i>	CIB8042905	Male	Shangcheng Co, Anhui Prov., China	136.9	67.4	19.7	15.0	52.0	6.3	3.7	8.4	11.7	2.1	4.9	8.1	9.6	7.4	5.9	13.2	7.0	5.8	69.5	7.8
<i>Tylosaurion dahicus</i>	CIB80526010	Male	Shangcheng Co, Anhui Prov., China	158.9	74.0	20.9	15.5	57.3	5.9	4.0	8.1	12.0	1.6	5.0	7.6	9.8	7.0	5.4	12.1	7.5	5.0	74.9	8.1
<i>Tylosaurion wuxianensis</i>	CIB2005062703	Female	Pingwu Co., Gansu Province, China	130.7	70.5	19.2	16.6	54.9	5.7	3.1	8.8	12.4	1.8	4.2	8.7	7.7	7.2	3.7	11.6	7.7	5.9	69.2	9.2
<i>Tylosaurion wuxianensis</i>	CIB200811CD06	Female	Yunyang Co., Chongqing City, China	143.7	77.6	19.2	15.4	62.2	6.1	3.3	8.2	12.7	2.2	5.2	8.8	10.0	8.3	5.5	11.7	8.1	6.0	68.9	6.1
<i>Tylosaurion wuxianensis</i>	CIB200811CD07	Female	Yunyang Co., Chongqing City, China	137.1	74.9	21.0	18.1	62.0	6.0	3.5	7.9	12.4	1.5	4.7	8.0	8.7	8.1	5.3	11.6	7.9	6.1	66.3	8.0
<i>Tylosaurion wuxianensis</i>	CIB7405	Female	Pingwu Co, Gansu Province, China	124.1	66.3	18.5	16.0	51.8	5.7	4.2	8.8	11.8	1.9	4.9	8.6	9.0	8.3	4.6	13.0	7.5	5.0	60.6	8.2
<i>Tylosaurion wuxianensis</i>	CIB74073	Female	Pingwu Co, Gansu Province, China	137.4	73.2	18.4	17.4	60.3	6.2	3.8	8.6	12.9	1.9	4.8	7.7	8.4	6.8	4.2	11.2	8.5	5.9	64.9	8.9
<i>Tylosaurion wuxianensis</i>	CIB200811CD03	Male	Yunyang Co., Chongqing City, China	117.1	71.0	17.6	15.0	53.3	5.9	3.7	8.4	11.5	1.6	5.0	8.7	11.0	6.2	5.2	11.4	7.4	6.5	48.8	5.0
<i>Tylosaurion wuxianensis</i>	CIB74074	Male	Pingwu Co., Gansu Province, China	122.8	61.0	19.9	16.3	50.5	5.5	3.7	8.4	12.6	1.8	4.7	8.4	9.0	7.3	4.9	12.0	7.8	5.6	58.4	8.4
<i>Tylosaurion anhuiensis</i>	AHU-16-EE-001	Male	Yuexi Co, Anhui Prov., China	119.8	66.7	15.3	13.8	53.3	3.0	3.7	/	/	/	/	7.0	/	/	/	/	/	/	53.2	7.6
<i>Tylosaurion anhuiensis</i>	AHU-16-EE-002	Male	Yuexi Co, Anhui Prov., China	124.8	68.4	15.4	13.6	52.3	3.2	3.6	/	/	/	/	7.5	/	/	/	/	/	/	56.4	7.2
<i>Tylosaurion anhuiensis</i>	AHU-13-EE-005	Male	Yuexi Co, Anhui Prov., China	125.9	63.5	14.7	13.2	51.0	4.0	3.5	/	/	/	/	6.5	/	/	/	/	/	/	56.2	6.8
<i>Tylosaurion anhuiensis</i>	AHU-16-EE-007	Male	Yuexi Co, Anhui Prov., China	132.3	70.0	14.9	14.6	56.3	3.6	3.8	/	/	/	/	6.7	/	/	/	/	/	/	63.6	8.1
<i>Tylosaurion anhuiensis</i>	AHU-16-EE-011	Male	Yuexi Co, Anhui Prov., China	123.1	71.7	16.1	14.1	57.7	3.5	3.5	/	/	/	/	7.0	/	/	/	/	/	/	59.6	7.7
<i>Tylosaurion anhuiensis</i>	AHU-16-EE-014	Male	Yuexi Co, Anhui Prov., China	133.5	70.0	17.0	14.8	55.9	3.5	4.1	/	/	/	/	6.8	/	/	/	/	/	/	61.0	8.0
<i>Tylosaurion anhuiensis</i>	AHU-13-EE-020	Male	Yuexi Co, Anhui Prov., China	130.4	68.4	14.4	13.6	53.5	3.4	3.8	/	/	/	/	7.4	/	/	/	/	/	/	60.3	8.0
<i>Tylosaurion anhuiensis</i>	AHU-16-EE-026	Male	Yuexi Co, Anhui Prov., China	131.8	70.0	16.4	14.6	55.3	3.1	3.2	/	/	/	/	7.9	/	/	/	/	/	/	64.7	6.0

Table S2 Uncorrected p -distances between the *T. ylotriton sensu lato* species based on the 16S gene (upper triangular matrix) and 16S+ND2 dataset (lower triangular matrix).

ID	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
1	<i>Tylotriton maolanensis</i> sp.nov.		0.010	0.016	0.012	0.008	0.008	0.018	/	0.042	0.028	/	0.038	0.044	0.046	0.046	0.044	/	/	/	0.036	/	/	0.050	0.056	0.044	0.034	0.030
2	<i>Tylotriton broadoridgus</i>	0.022		0.010	0.010	0.007	0.012	0.018	/	0.042	0.032	/	0.036	0.046	0.046	0.048	0.046	/	/	/	0.040	/	/	0.050	0.056	0.046	0.036	0.040
3	<i>Tylotriton dabienicus</i>	0.028	0.026		0.012	0.013	0.018	0.024	/	0.042	0.040	/	0.044	0.056	0.056	0.056	0.054	/	/	/	0.044	/	/	0.052	0.064	0.056	0.042	0.046
4	<i>Tylotriton anhuiensis</i>	0.025	0.027	0.029		0.009	0.014	0.020	/	0.042	0.036	/	0.040	0.048	0.052	0.052	0.046	/	/	/	0.040	/	/	0.050	0.056	0.048	0.038	0.042
5	<i>Tylotriton wuxianensis</i>	0.029	0.031	0.036	0.030		0.010	0.013	/	0.041	0.028	/	0.033	0.044	0.044	0.044	0.042	/	/	/	0.036	/	/	0.047	0.053	0.044	0.030	0.034
6	<i>Tylotriton luyangensis</i>	0.048	0.051	0.054	0.052	0.050		0.020	/	0.043	0.030	/	0.040	0.046	0.048	0.048	0.046	/	/	/	0.038	/	/	0.052	0.058	0.046	0.036	0.032
7	<i>Tylotriton lizhenchangi</i>	0.059	0.062	0.066	0.062	0.057	0.055		/	0.043	0.030	/	0.032	0.050	0.046	0.046	0.044	/	/	/	0.042	/	/	0.052	0.058	0.050	0.030	0.036
8	<i>Tylotriton panhai</i>	0.100	0.094	0.094	0.095	0.101	0.094	0.098	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/
9	<i>Tylotriton vietnamensis</i>	0.086	0.087	0.086	0.086	0.082	0.086	0.092	0.112		0.044	/	0.042	0.046	0.050	0.052	0.050	/	/	/	0.046	/	/	0.048	0.053	0.046	0.040	0.038
10	<i>Tylotriton hainanensis</i>	0.063	0.062	0.072	0.064	0.068	0.062	0.068	0.097	0.086	/		0.014	0.044	0.042	0.040	0.038	/	/	/	0.034	/	/	0.048	0.054	0.044	0.032	0.032
11	<i>Tylotriton notialis</i>	0.079	0.079	0.086	0.081	0.086	0.085	0.096	0.102	0.118	0.046	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/
12	<i>Tylotriton asperimus</i>	0.068	0.069	0.074	0.068	0.069	0.071	0.080	0.111	0.086	0.038	0.053		0.054	0.050	0.048	0.046	/	/	/	0.044	/	/	0.054	0.060	0.054	0.040	0.038
13	<i>Tylotriton zieglerti</i>	0.070	0.068	0.077	0.069	0.073	0.072	0.084	0.100	0.090	0.044	0.048	0.047		0.026	0.028	0.032	/	/	/	0.022	/	/	0.034	0.027	0.000	0.036	0.036
14	<i>Tylotriton verrucosus</i>	0.081	0.084	0.091	0.088	0.079	0.085	0.092	0.126	0.098	0.083	0.110	0.094	0.084		0.006	0.018	/	/	/	0.020	/	/	0.036	0.037	0.026	0.032	0.030
15	<i>Tylotriton shanjing</i>	0.081	0.084	0.091	0.086	0.081	0.086	0.093	0.127	0.099	0.082	0.110	0.092	0.085	0.010		0.012	/	/	/	0.018	/	/	0.034	0.035	0.028	0.032	0.030
16	<i>Tylotriton pulcherrimus</i>	0.078	0.081	0.087	0.081	0.075	0.081	0.087	0.121	0.096	0.076	0.102	0.088	0.081	0.020	0.021		/	/	/	0.018	/	/	0.038	0.039	0.032	0.030	0.030
17	<i>Tylotriton podichthys</i>	0.098	0.100	0.106	0.097	0.095	0.101	0.112	0.123	0.129	0.101	0.107	0.108	0.107	0.041	0.043	0.037	/	/	/	/	/	/	/	/	/	/	/
18	<i>Tylotriton uyenoii</i>	0.124	0.128	0.131	0.126	0.124	0.126	0.129	0.144	0.148	0.125	0.127	0.129	0.133	0.072	0.072	0.068	0.082	/	/	/	/	/	/	/	/	/	/
19	<i>Tylotriton anguliceps</i>	0.107	0.109	0.119	0.107	0.107	0.101	0.123	0.129	0.130	0.100	0.107	0.113	0.108	0.043	0.043	0.040	0.053	0.072	/	/	/	/	/	/	/	/	/
20	<i>Tylotriton yangi</i>	0.076	0.081	0.087	0.081	0.077	0.076	0.088	0.125	0.096	0.075	0.103	0.083	0.075	0.033	0.035	0.031	0.051	0.075	0.042	/	/	/	0.022	0.031	0.022	0.034	0.034
21	<i>Tylotriton shanorum</i>	0.103	0.101	0.109	0.107	0.111	0.103	0.118	0.124	0.122	0.098	0.109	0.113	0.109	0.062	0.066	0.062	0.074	0.091	0.067	0.064	/	/	/	/	/	/	/
22	<i>Tylotriton ngarsuensis</i>	0.113	0.114	0.122	0.118	0.119	0.113	0.128	0.131	0.129	0.108	0.120	0.122	0.119	0.070	0.073	0.070	0.082	0.100	0.077	0.072	0.018	/	/	/	/	/	/
23	<i>Tylotriton himalayanus</i>	0.086	0.086	0.091	0.088	0.086	0.085	0.094	0.123	0.101	0.081	0.105	0.095	0.085	0.055	0.053	0.054	0.068	0.085	0.069	0.051	0.050	0.064	0.025	0.034	0.044	0.048	
24	<i>Tylotriton kachinorum</i>	0.054	0.055	0.063	0.055	0.052	0.057	0.057	0.200	0.053	0.053	0.200	0.059	0.026	0.037	0.035	0.039	0.000	0.000	0.000	0.031	0.000	0.000	0.024	0.027	0.045	0.045	
25	<i>Tylotriton kweichowensis</i>	0.078	0.075	0.087	0.081	0.080	0.079	0.088	0.107	0.096	0.072	0.100	0.086	0.062	0.047	0.049	0.047	0.061	0.080	0.062	0.049	0.059	0.070	0.047	0.026	0.036	0.036	
26	<i>Tylotriton taliangensis</i>	0.070	0.074	0.075	0.072	0.068	0.072	0.073	0.105	0.088	0.068	0.091	0.075	0.075	0.061	0.060	0.059	0.077	0.100	0.084	0.064	0.081	0.091	0.065	0.045	0.055	0.012	
27	<i>Tylotriton pseudoverrucosus</i>	0.071	0.075	0.079	0.077	0.073	0.071	0.079	0.104	0.091	0.068	0.089	0.077	0.074	0.060	0.062	0.055	0.072	0.100	0.085	0.061	0.079	0.087	0.063	0.045	0.052	0.022	